

Introduction

WALTER D. KOENIG AND JANIS L. DICKINSON

University of California, Berkeley

Cooperative breeding continues to engender considerable interest among behavioral ecologists. However, the players and issues have changed dramatically since the publication of the first *Cooperative Breeding in Birds* volume (Stacey and Koenig 1990a). Back then, a series of long-term demographic studies were coming to fruition, opening the door for a synthetic volume that would “search for common themes and patterns” while illustrating “the great diversity that exists among cooperatively breeding birds” (Stacey and Koenig 1990b). At the time it appeared that the “common themes and patterns” would outstrip the “great diversity” and that a general understanding of the main issues raised by the phenomenon of cooperative breeding was about to be achieved (Emlen 1997a).

Such optimism concerning a general answer to the paradox of helping behavior was quickly dismissed (Cockburn 1998), and it has continued to elude our grasp. Instead, new theoretical approaches and studies have emerged to reinvigorate the field. Three stand out in particular. First is DNA fingerprinting, which was just getting started in the late 1980s and was only minimally represented in the 1990 volume. Multilocus minisatellite fingerprinting and its descendant, microsatellite fingerprinting, provided the long-sought-after ability to determine parentage and estimate relatedness. Fingerprinting allowed those who were continuing long-term studies or who had been fortunate enough to collect and save blood samples either to confirm prior inferences regarding patterns of parentage (as in Florida scrub-jays and acorn woodpeckers: Quinn *et al.* 1999; Dickinson *et al.* 1995; Haydock *et al.* 2001) or to turn all prior inference on its head (as in the splendid fairy-wren: Brooker *et al.* 1990). This latter case was particularly dramatic, since it made what was already a perplexing mating system (Rowley *et al.* 1986) even more extra-

ordinary. More importantly, it raised questions about all other presumptions about paternity based on banding of cooperative breeders: no longer would it be possible to assume that the mating system of a cooperative breeder would necessarily bear close correspondence to the demographically observed social unit.

Unfortunately, inferring parentage (as opposed to performing paternity exclusion analyses) is still not easy in birds, particularly in cooperative breeders, where potential sires (or dams) are close relatives. Consequently, the number of studies of cooperative breeders with unambiguous data on parentage is still relatively small. However, the conclusion from studies performed thus far, discussed by Cockburn (Chapter 5), is clear: diversity rules. Explaining this diversity remains a challenge, and is likely to become even more difficult as additional data on other species become available.

Second has been the consistent failure of attempts to predict the occurrence of cooperative breeding based on ecological features or life-history characteristics (Dow 1980; Yom-Tov 1987; Brown 1987; Ford *et al.* 1988; Du Plessis *et al.* 1995; Cockburn 1998). This is not to say that ecological factors are unimportant (Chapter 3), or that cooperative breeders do not share a variety of ecological and life-history characteristics (Chapter 14). However, many of the characteristics shared by cooperative breeders, such as year-round residency, prolonged dependence of offspring, and even ecological constraints on dispersal, are found in many non-cooperative breeders as well. In other words, we can often do a reasonable job of answering the question of why a particular species is a cooperative breeder, but we continue to be abject failures at offering a convincing explanation for why many other species are *not* cooperative breeders.

The third, and perhaps the most important, factor generating renewed excitement in the field of

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cooperative breeding has been the new generation of field studies that began yielding important results in the 1990s. Notable among these was work on the Seychelles warbler, the long-tailed tit, the Siberian jay, and the onslaught of work on various Australian cooperative breeders seemingly competing to be designated “most bizarre,” including the inimitable fairy-wrens, the white-winged chough, the white-browed scrub-wren, noisy and bell miners, the eclectus parrot, and more. These systems simply cannot be assimilated into prior frameworks concerning the evolution of cooperative breeding based on work summarized in Stacey and Koenig (1990a).

The bottom line is that we have more questions, and fewer answers, to the central questions in the field of cooperative breeding than we did a decade ago. Furthermore, the field has progressed conceptually as well as empirically, leading to novel ways of analyzing new genetic and old demographic data. As the genetic data and their interpretations are not yet available for many of the newer studies, we felt that a thematic volume based on major concepts and issues was more timely than a follow-up compilation focused on individual species. The current volume is the result of this effort.

Several of these theoretical issues are addressed explicitly. A good example is Jamieson's (1989, 1991) “unselected hypothesis,” which was just gathering steam (and controversy) as Stacey and Koenig (1990a) went to press. Although hammered at the level of functional consequences (Koenig and Mumme 1990; Emlen *et al.* 1991; Ligon and Stacey 1991), it has returned, stronger than ever, at the level of evolutionary, or phylogenetic, origins, and is discussed in detail by Ligon and Burt (Chapter 1).

At least two conceptual issues addressed here owe much of their recent development to advances in molecular biology similar to those that now allow determination of parentage. The first is the problem of sex allocation, an area poised for an explosion now that sexing techniques in birds have become relatively cheap and easy. Although research exploiting this breakthrough is still young, cooperative breeders are positioned to play a key role in testing hypotheses for sex allocation, an area that has continued to interest and befuddle workers ever since Fisher (1930) laid down the theoretical foundation that currently defines the field. Progress in this area is summarized by Komdeur (Chapter 6).

The second is how reproduction is partitioned among individuals within social groups. This may or may not be an issue among the “simpler” cooperative breeders in which groups consist of pairs with non-breeding helpers that are constrained in their reproductive activities by incest avoidance (Chapter 9). However, things become considerably more complicated in species in which groups contain more than one potential breeder of one or both sexes. In fact, even describing such systems can be a challenge.

Compare three groups of acorn woodpeckers, each of which contains one breeder female and two males. In group 1, male 1 is an unrelated immigrant from elsewhere that bred with the female the previous year and produced one surviving male offspring that stayed in the natal group and became male 2. In the other two groups, the two males are brothers that immigrated into the group together. All groups breed. In group 1, male 1 sires all the young, since male 2, the helper, is constrained from breeding by incest avoidance (Chapter 9). In groups 2 and 3, neither male is constrained by incest avoidance and both mate-guard and attempt to mate with the female. In group 2 only male 1 is successful in siring young in the nest, whereas in group 3 there is multiple paternity and both males successfully sire offspring. Group 1 is a standard cooperatively breeding group with a single non-breeding helper male, while group 3 is a cooperatively polyandrous group with two cobreeder males. But where does group 2 fit in?

Both males in group 2 were potential mates of the female, even though one failed to sire any offspring. In terms of his genetic contribution, this unsuccessful male is equivalent to the non-breeding helper in group 1, since neither sired any offspring in the nest. Both are related to the nestlings indirectly through male 1 (to which both male 2s are genetically related).

The two males do, however, differ in two ways: relatedness to the chicks, which is higher for the non-breeding helper since he is also related to the nestlings through the breeder female, and copulatory access to the female, which the potential cobreeder may have had even though he was not successful in siring offspring. Unless the potential cobreeder has perfect information regarding his paternity in the nest, his behavior toward the nestlings should be influenced by the possibility that he may have sired at least some offspring (even if he did not).

In contrast, the non-breeding helper has been exposed to strong selection to avoid engaging in reproductive activities with his mother because of incest avoidance, and his treatment of nestlings should not be affected by his mating access.

Such complexities continue to result in considerable differences in the field. This starts immediately with the definition of cooperative breeding, defined inclusively by Cockburn (Chapter 5) to include all three hypothetical groups, but more exclusively by Ligon and Burt (Chapter 1) to include only groups containing non-breeding helpers. This latter definition clearly eliminates our hypothetical group 3; how it deals with the problem of group 2 is less clear.

In any case, cooperative breeders in which groups contain more than one potential breeder raise the theoretically important issue of how reproduction is partitioned. This field of “reproductive skew” was originally developed by Vehrencamp (1979, 1983a, 1983b) well before Stacey and Koenig (1990a). However, relatively little could be done empirically with skew theory until methods of determining parentage were developed. Availability of parentage data led to an explosion of interest, both empirically and theoretically. The impact of reproductive skew theory on our understanding of cooperative breeding systems is addressed extensively by Magrath *et al.* (Chapter 10) and by Vehrencamp and Quinn (Chapter 11), who focus more generally on joint nesting systems.

Other chapters presented here focus on issues that were controversial in Stacey and Koenig (1990a) and have remained so since. Why, in cooperative breeders, do helpers delay dispersal? And why, once dispersal is delayed, do they help? A general answer to the first of these questions once appeared to be within our grasp. This answer involved “ecological constraints,” which were poised as a major factor in the evolution of cooperative breeding despite some controversy (Stacey and Ligon 1987, 1991). Although “ecological constraints” are clearly important in many cooperative breeding species, non-complementary alternatives have since surfaced, including nepotism and other “benefits of philopatry” that appear to be particularly important in species with delayed dispersal and no helping behavior. Ekman *et al.* (Chapter 2) bring us up to date on this important issue.

But what about helping behavior itself? At the time of Stacey and Koenig (1990a), the major issue was the

importance of kin selection (indirect fitness benefits), brought to the forefront because the vast majority of cooperative breeding systems are family-based. Yet direct fitness benefits may be far more important than previously suspected, an hypothesis explored by Heinsohn (Chapter 4). Still there is debate over the relative importance of direct and indirect benefits and the quality of evidence for various costs and benefits of helping behavior that have been addressed over the years, as evidenced by the different viewpoints taken by Heinsohn (Chapter 4) as compared to Dickinson and Hatchwell (Chapter 3).

A long-standing issue that is revisited in this volume is that of incest, which is a potential problem due to the high relatedness among group members in most cooperative breeders. Does this result in rampant inbreeding, or at least a higher incidence of incest than in non-cooperative species? Although controversy remains, recent studies, many making use of molecular techniques to determine parentage, have in general presented a unified front supporting a central role of incest avoidance as a determinant of reproductive roles in cooperative breeding societies. The saga leading to this conclusion, along with a discussion of studies and investigators challenging this interpretation, is discussed by Koenig and Haydock (Chapter 9).

One of the more important ways that the study of cooperative breeding has diversified since Stacey and Koenig (1990a) has been its expansion into questions directed at levels of analysis other than that of ultimate fitness consequences. Besides evolutionary origins, discussed by Ligon and Burt (Chapter 1), the role of physiological constraints in cooperative breeders is summarized by Du Plessis (Chapter 7), while the hormonal correlates of cooperative breeding are reviewed by Schoech *et al.* (Chapter 8). The latter, in particular, offer several excellent examples in which physiological traits are modified to facilitate helping behavior, a finding that counters the original “unselected hypothesis”: regardless of how it originated, helping behavior is clearly under strong selection in many species and is correlated with numerous physiological adaptations.

Two additional issues, largely ignored in Stacey and Koenig (1990a), are covered in detail here. First, Walters *et al.* (Chapter 12) discuss reasons why cooperative breeders are of particular interest to the emerging field of conservation biology and how these species are faring relative to non-cooperative breeders in the

face of expanding threats of habitat loss and fragmentation. As they point out, many cooperative breeders exhibit traits that potentially make them uniquely vulnerable to such threats, including philopatry, small population size, and specific habitat requirements. On the other hand, populations of cooperative breeders typically contain relatively large numbers of “extra” adults in the form of nonbreeding helpers, which can in some cases buffer against the effects of demographic stochasticity. Whether these and other life-history characteristics make cooperatively breeding species more or less vulnerable to habitat loss and fragmentation is an important issue that Walters *et al.* discuss for the first time.

Second is work that has been done on mammals. Although the chapters in Stacey and Koenig (1990a) were restricted to avian systems, studies in other taxa have contributed significantly to our understanding of cooperative breeding, to the extent that a parallel volume devoted to mammalian cooperative breeding was published several years later (Solomon and French 1997). Acknowledging these contributions, we enlisted Russell (Chapter 13), one of the few workers to have experience in both avian and mammalian cooperative systems, to discuss ways in which study of the latter has contributed, both theoretically and empirically, to our understanding of cooperative breeding in general.

We conclude with a summary by Pruett-Jones (Chapter 14), who generates a series of 13 synthetic statements about cooperative breeding with which all workers in the field, or at least the majority, can agree. Although not the synthesis that seemed so close back in 1990, his chapter offers as close to a set of common patterns among cooperative breeders as has ever been conceived, leaving considerable hope that a general understanding of this phenomenon may exist after all, despite the ever greater diversity being discovered in such systems.

We did not start out with the goal of either excluding contributors to Stacey and Koenig (1990a) or highlighting younger workers. However, many of the new ideas and data that have continued to draw attention to the field have come from a new generation of investigators, as evidenced by the relatively low overlap between the two volumes, which share only four authors in common. This high proportion of “new blood” is part of what has kept the field of cooperative breeding dynamic and active. It has also helped generate new controversies, many of which are highlighted in the chapters presented here. Our hope is that these chapters, and the alternative viewpoints they present, will provide yet another generation of students with the same kind of excitement and inspiration that we experienced when first discovering this field.

1 • Evolutionary origins

J. DAVID LIGON

University of New Mexico

D. BRENT BURT

Stephen F. Austin State University

Cooperative breeding (hereafter often abbreviated as CB) is an umbrella label that includes a diverse array of mating and social systems (Ligon 1999). For example, Brown (1987) lists 13 separate categories of CB (see also Chapter 5). The variability in the forms of CB is due to differences in both the strength and the forms of selection on helping behaviors, mating strategies, and other aspects of group living. Here we follow the commonly employed definition of avian cooperative breeding, which is that it involves the existence of social units composed of two or more breeding birds, plus one or more (often presumed) non-breeding “helpers-at-the-nest” (Brown 1987; Edwards and Naeem 1993). It is the feeding of young birds by the helpers – also referred to as alloparental behavior – that characterizes cooperative breeding and that has made it of singular interest.

For most of the history of CB studies, researchers have sought ecological factors that might have promoted the evolutionary development of CB. This search has met with limited success, in part because ecological and climatic considerations, in themselves, offer little predictive power beyond the fact that north-temperate-zone species are unlikely to be cooperative breeders (Heinsohn *et al.* 1990; Mumme 1992a; Cockburn 1996). Even in tropical and subtropical areas, where cooperative breeders occur most frequently, one typically cannot offer a good guess, based solely on environmental conditions, as to whether or not a given species will prove to exhibit CB. The only factor that does provide good predictive power is whether the species in question has cooperatively breeding relatives. This suggests that phylogenetic history may be a critical consideration in any attempt to address the origins and, to a lesser extent, the maintenance of cooperative breeding.

IDENTIFYING COOPERATIVE BREEDING AND THE ISSUE OF HOMOLOGY

Some writers have lumped a wide array of social and genetic mating systems under the label of cooperative breeding (Brown 1987; Hartley and Davies 1994; Arnold and Owens 1998, 1999). This is understandable to the extent that the social and sexual relationships among members of a group are often not well known. In some cases, individuals that first were assumed to be non-breeding helpers have, with the use of molecular techniques, been shown to breed, albeit rarely (Rabenold *et al.* 1990; Haydock *et al.* 1996). This dichotomy between actual non-breeding helpers (usually the offspring of one or both members of the breeding pair) and would-be breeders is clearly seen in pied kingfishers. In this species, “primary” helpers typically are offspring of the nesting pair and they do not attempt to mate with a parent. In contrast, “secondary” helpers are unmated, unrelated males that may, depending on circumstances, form a pair bond with the breeding female at a later date (Reyer 1990). Both primary and secondary helpers deliver food to nestlings.

In other social mating systems, all members of a social unit are breeders or potential breeders; the “goal” for each group member is actual parentage. For example, in dunnock groups all members are actual or hopeful breeders (Davies 1990). There are no non-breeding “helpers,” even though a beta male may not have sired any offspring during a particular nesting attempt (see also Chapter 5). The term polygynandry more accurately labels the dunnock’s unusually variable social-mating system than does cooperative breeding.

In still other cases, both non-breeding helpers and breeders or would-be breeders occur in the same social

unit (Haydock *et al.* 1996). If there has been no selection to preferentially feed one's own chicks, one could argue that the role played by the prospective breeders is no different than the role of the true helpers, despite the fact that any selective benefits may differ: both feed nestlings that are not their own offspring.

The rule we follow here for including a given species is that non-breeding helpers occur within a social unit beyond the primary pair, irrespective of the presence or absence of potential breeders. This approach is weakened by the scanty knowledge we have of genetic parentage in most species that appear to breed cooperatively. We feel that this weakness is offset, however, by obtaining a clearer focus on the phenomenon of interest here, the feeding of chicks by individuals that have little or no possibility of parentage within the brood they are provisioning.

Another important point relates to the issue of homology. Is the CB reported for an ecologically and taxonomically diverse array of species homologous? In other words, is CB across different species and lineages derived from a common ancestor, or has it appeared *de novo* in different lineages? This is one of the most interesting and difficult questions we attempt to address in this chapter. We argue below that for altricial groups, the answer ultimately depends on whether or not altriciality evolved one or more times. If the altriciality of the groups we consider is derived from a common ancestor, then it would be appropriate to view the concomitant intense parental care shared by these groups as homologous.

Conversely, if it could be shown that altriciality evolved separately from precocity in two or more of these lineages (the coraciiform and passeriform birds, for example), one might argue that the associated parental care exhibited by these two groups reflects analogy rather than homology. In either case, we argue that the intense parental care associated with altricial lineages predisposed individuals to alloparental care, given close proximity of non-breeders and begging young. In other words, altriciality and alloparental care evolved essentially in concert, but alloparental care (excluding the hosts of social parasites) is normally unexpressed in descendant lineages in which individuals typically have no close contact with young birds that are not their own offspring.

EVOLUTIONARY ORIGIN VERSUS EVOLUTIONARY MAINTENANCE

The issue of its evolutionary origin has been largely ignored for most of the modern history of the study of CB. Rather, the level of analysis (Sherman 1988) on which most students of this phenomenon focused was the current adaptive significance of CB, sometimes assuming that the environmental factors promoting or maintaining CB in the particular species they studied also accounted for its evolutionary origin.

The appearance of a number of publications that considered phylogenetic history (Russell 1989; Peterson and Burt 1992; Edwards and Naeem 1993; Ligon 1993, 1999; Farley 1995; Burt 1996; Cockburn 1996) clearly demonstrated the importance of distinguishing between evolutionary origins of CB and current maintenance of this trait. Why is this important? First, identifying the patterns of CB evolution provides us with opportunities for further study. For example, are certain environmental, behavioral or life history features associated with the origin or expression of CB? Second, when the ecological correlates associated with CB change, do we see a subsequent loss of CB? If so, this pattern implies that specific ecological factors play an important role in the maintenance of CB. Alternatively, if transitions from CB to non-CB do not occur under different ecological conditions, three interpretations are possible: (1) specific ecological settings are not a primary factor in the maintenance of CB as an adaptive social system, (2) CB is adaptive in different ways in a variety of ecological circumstances, or (3) CB is not adaptive in at least some of the species exhibiting it (Ligon and Stacey 1989).

An evolutionary framework also provides a fresh perspective on the interaction between the two most widely recognized aspects of CB, delayed dispersal and helping behavior. For example, life-history characteristics associated with delayed dispersal have recently been identified as important in the origins of CB (Arnold and Owens 1998). However, alloparental care may initially have been nothing more than a response to the stimuli of begging nestlings (Jamieson and Craig 1987a; Jamieson 1989). In such cases, although the breeding system fits the definition of CB, at this initial evolutionary stage CB as a "trait" is simply an epiphenomenon of delayed dispersal. When alloparental care subsequently

became adaptive in certain group-living lineages, the various forms of CB could be labeled as “exaptations” (Gould and Vrba 1982). That is, delayed dispersal was the original, adaptive response to particular ecological or physiological circumstances that provided the opportunity for alloparental behavior among related individuals, but subsequent benefits associated with helping behaviors give CB a new exaptive role.

The initial evolution of intense parental care associated with production of altricial young, together with group living, was the raw material for the subsequent adaptive development of CB. Ecological factors over the tens of millions of years from the early Tertiary to the present have modified this behavior in many ways, including, for a majority of altricial lineages, the absence of strong alloparental tendencies, or at least the absence of the regular expression of the behavior. However, in the ancestors of other species, those recognized today as regular or frequent cooperative breeders, the feeding of nestlings by non-parents set the stage for the development of a whole suite of adaptive modifications associated with CB, many of which are treated in this volume.

EVOLUTIONARY ORIGINS OF COOPERATIVE BREEDING

The origins of altriciality

Because the initial appearance of intense parent care, including parental feeding, must have been critically linked to the altricial mode of chick development, we first consider the origins of altriciality. Traditionally, the usual assumption has been that among birds as a whole precocity was the evolutionary precursor of altriciality (Gill 1995). However, Starck and Ricklefs (1998; Ricklefs and Starck 1998) mapped chick developmental mode onto the phylogeny of Sibley and Ahlquist (1990) and concluded that altricial development is probably ancestral for the infraclass Neoaves (which includes all modern bird lineages) except the ratite–anseriform clade and the turniciform lineage (Fig. 1.1). Ricklefs and Starck (1998) suggested that within the Neoaves precocity has re-evolved in both the superorder Strigimorphae and the common ancestor of the orders Gruiformes and Ciconiiformes. Altriciality has then again re-evolved

numerous times within the Ciconiiformes. These multiple evolutionary transitions probably account for the variability along the altriciality–precocity spectrum among living groups of Neoaves. For purposes of this chapter, the key point is that while altriciality may or may not be ancestral in birds as a whole, it probably is ancestral in all but the two most basal major avian lineages (Fig. 1.1).

Did types of birds likely to produce altricial young exist during the early history of modern birds? Avian evolution during the Paleocene and early Eocene apparently was explosive, with most modern types except the passerines appearing in the fossil record between the end of the Cretaceous and the lower Eocene, a period of only about 13 million years (Feduccia 1996). Many small arboreal or aerial species existed by this time (Mayr 2000, 2001), which strongly suggests that fully altricial young had evolved even earlier. This is because chicks of such species probably could not have been sufficiently precocial and mobile at hatching to accompany their parents as they foraged. In fact, the altricial condition may have initially evolved in response to the development of arboreal and aerial lifestyles of small, actively feeding lineages (Ricklefs and Starck 1998). In short, specialized parental care, including the delivery of food to the mouths of nestlings, was a key requisite for the evolution of altricial young and, based on the types of birds present at that time, probably was already well developed by the early Tertiary.

In summary, the analyses of Starck and Ricklefs lead to the conclusion that altriciality is ancient and, by implication, that intense parental care of helpless young is also an ancient adaptation. Finally, in support of this point, a number of altricial groups (the parvclass Coraciae, including coraciiforms, galbuliforms, bucerotiforms, upupiforms, trogoniforms, as well as the piciforms and the colliiforms) are among the oldest neoavian lineages with living descendants (Sibley and Ahlquist 1990). Some of these groups contain a number of species that breed cooperatively (Fig. 1.1).

We used the concentrated changes test (Maddison 1990) in MacClade 4.0 (Maddison and Maddison 2000) to test our assertion that altriciality influences the evolution of CB. Multiple equally parsimonious reconstructions between breeding system states were found and optimization options were utilized to demonstrate the

a

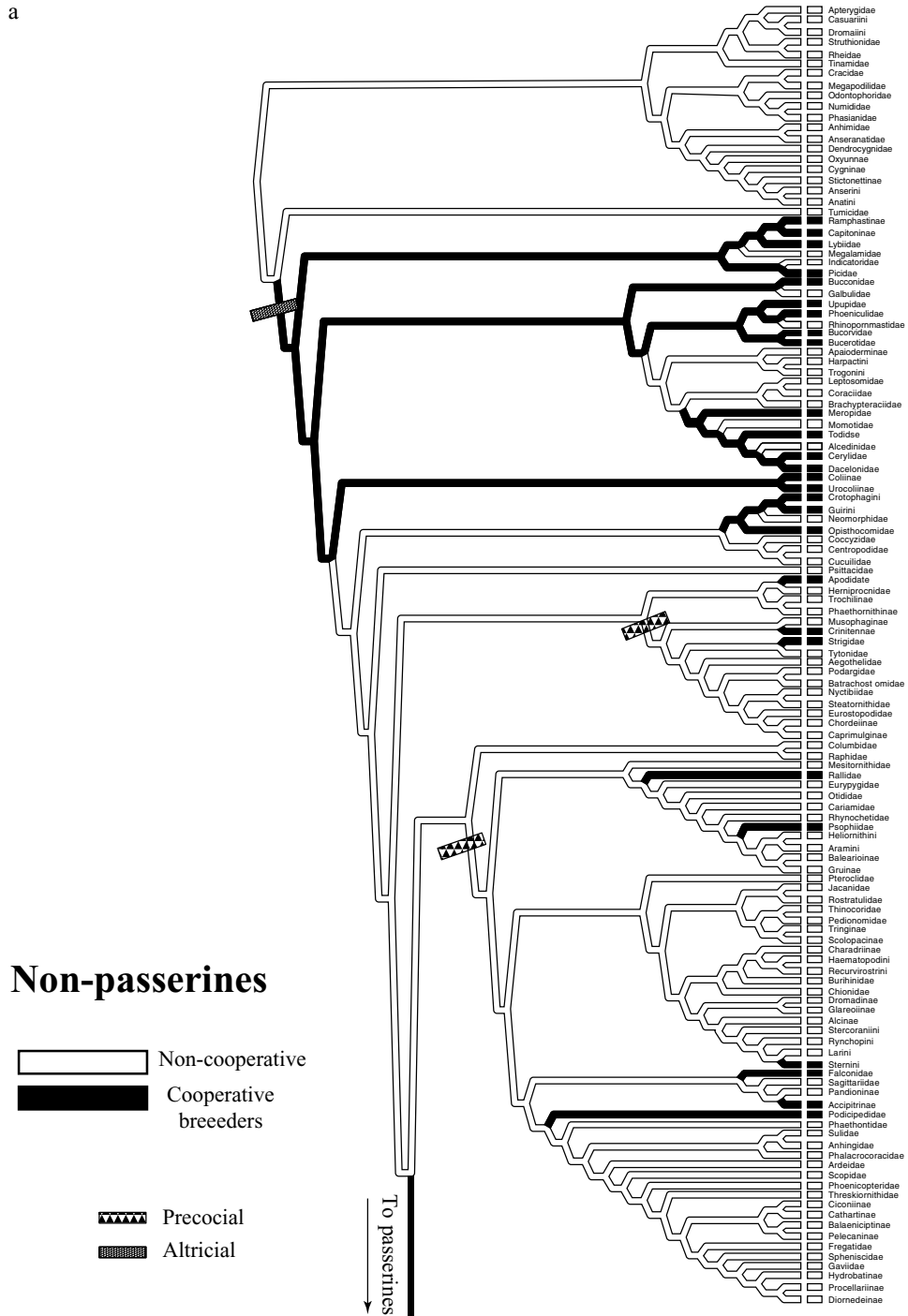


Figure 1.1. Reconstructed evolutionary transitions in breeding systems and developmental modes between lineages on the phylogeny of Sibley and Ahlquist (1990). Reconstruction on the (a) non-passerine portion and (b) passerine portion of the avian tree. Assuming this ACCTRAN reconstruction, transitions from

non-CB to CB occur more frequently ($P = 0.10$) on altricial branches than one would expect at random (concentrated changes test, Maddison 1990). The DELTRAN reconstruction (not shown) indicates a highly significant concentration of CB gains on altricial branches ($P = 0.01$).

b

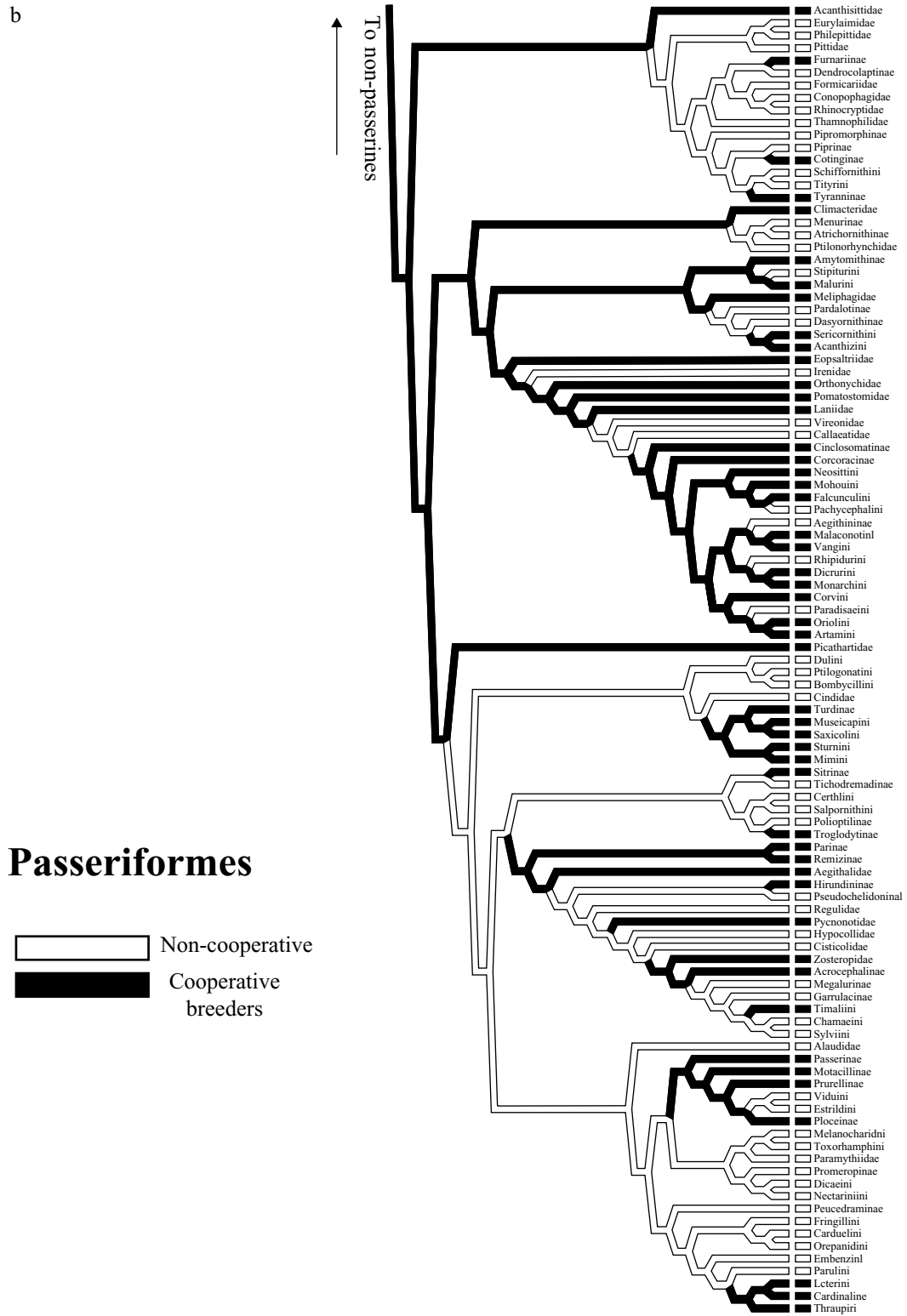


Figure 1.1. (cont.)

range of reconstructions that placed transitions from non-CB to CB either as close to the base of the tree as possible (ACCTTRAN option, Fig 1.1) or as close to the tips of the tree as possible (DELTRAN option, not shown).

The ACCTTRAN reconstruction of breeding system evolution (Fig. 1.1) shows 28 gains of CB (non-CB to CB) and 20 losses of CB (CB to non-CB). Of the 28 gains, 20 are found in altricial lineages. The DELTRAN reconstruction produces 38 gains of CB and 12 losses of CB, with 30 of these gains found in altricial lineages. The concentrated changes test suggests transitions from non-CB to CB lineages occur more frequently in lineages having altricial development than one would expect if these traits evolved independently. That is, our reconstructions show more gains of CB in altricial lineages than would be expected if breeding system and developmental mode were evolving randomly relative to each other.

This test does not include likely transitions between developmental traits within the Ciconiiformes. However, given that a number of these lineages have likely evolved altriciality and that we currently have them reconstructed as precocial, our tests are conservative. The evolutionary pattern verified by these tests, that there is concordance between altriciality and CB, is not surprising. However, we feel the evolutionary relationship between CB and altricial development has often been underappreciated by past researchers.

Origins of sociality in certain lineages of cooperative breeders

A key aspect of the scenario we present here is that cooperative breeding may initially have arisen more or less incidentally in response to the evolution of altricial young and the existence of factors favoring group living. In the prior section we discussed the relationship between altriciality and the concomitant intense parental care that it demands. Here we offer some suggestions concerning the initial factors leading to social living.

In terms of percentage of species of a particular lineage exhibiting this behavior, CB is most prevalent in certain families of rather small, primarily arboreal groups of birds within the ancient orders Coliiformes, Coraciiformes, Upupiformes, Bucerotiformes, and Piciformes (Fig. 1.1).

What traits might have predisposed these ancient and primarily or exclusively tropical birds to live in

groups and possibly subsequently to become cooperative breeders? Physiological limitations of one sort or another may be a primary factor that led to group-living in some of these groups, at least some of which have unusually low basal metabolic rates. Energy conservation by cavity- and group-roosting green woodhoopoes is one example (Boix-Hinzen and Lovegrove 1998). Individuals of the highly social speckled mousebird also have been shown to benefit greatly both by group-clustering during the day and by group-roosting at night (McKechnie and Lovegrove 2001a, 2001b). An apparently similar relationship between group-roosting, social living, and CB can be seen in certain groups of cooperatively breeding passeriform birds, including the family Pomatostomidae and the genera *Turdoides*, *Campylorhynchus*, and *Daphoenositta*. Further discussion of the potential interplay between physiological limitations and the evolution of cooperative breeding can be found in Chapter 5.

To summarize, for cooperative breeders in several tropical non-passerine groups, one response to low nocturnal temperatures, or, in colies, even low diurnal temperatures, is social roosting or clustering in order to conserve energy. Although data are few, it is becoming increasingly clear that in some groups of tropical and subtropical birds the correlation between latitude and cooperative breeding (Brown 1974) is strongly affected by the relationship between social living and the behavioral and physiological characters affecting energy balance.

Origins of alloparental behavior

What factors promoted the initial appearance of cooperative breeding in the ancestors of today's cooperative breeders? Addressing this question requires consideration of the evolution and care of altricial chicks. Here we modify and extend the arguments of Jamieson and Craig (1987a), Jamieson (1989, 1991) and Ligon and Stacey (1989, 1991) concerning the origins of alloparental feeding.

We envision two likely evolutionary routes to CB. In the first, alloparental care is initially an epiphenomenon of delayed dispersal (generalized feeding response plus access to the stimuli of begging chicks), with subsequent modifications due to one or more of several possible selective advantages. This route is most applicable to territorial species living in situations where ecological conditions of one or more kinds either provide